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Growth of Regeneration Defoliated by Spruce Budworm in Idaho

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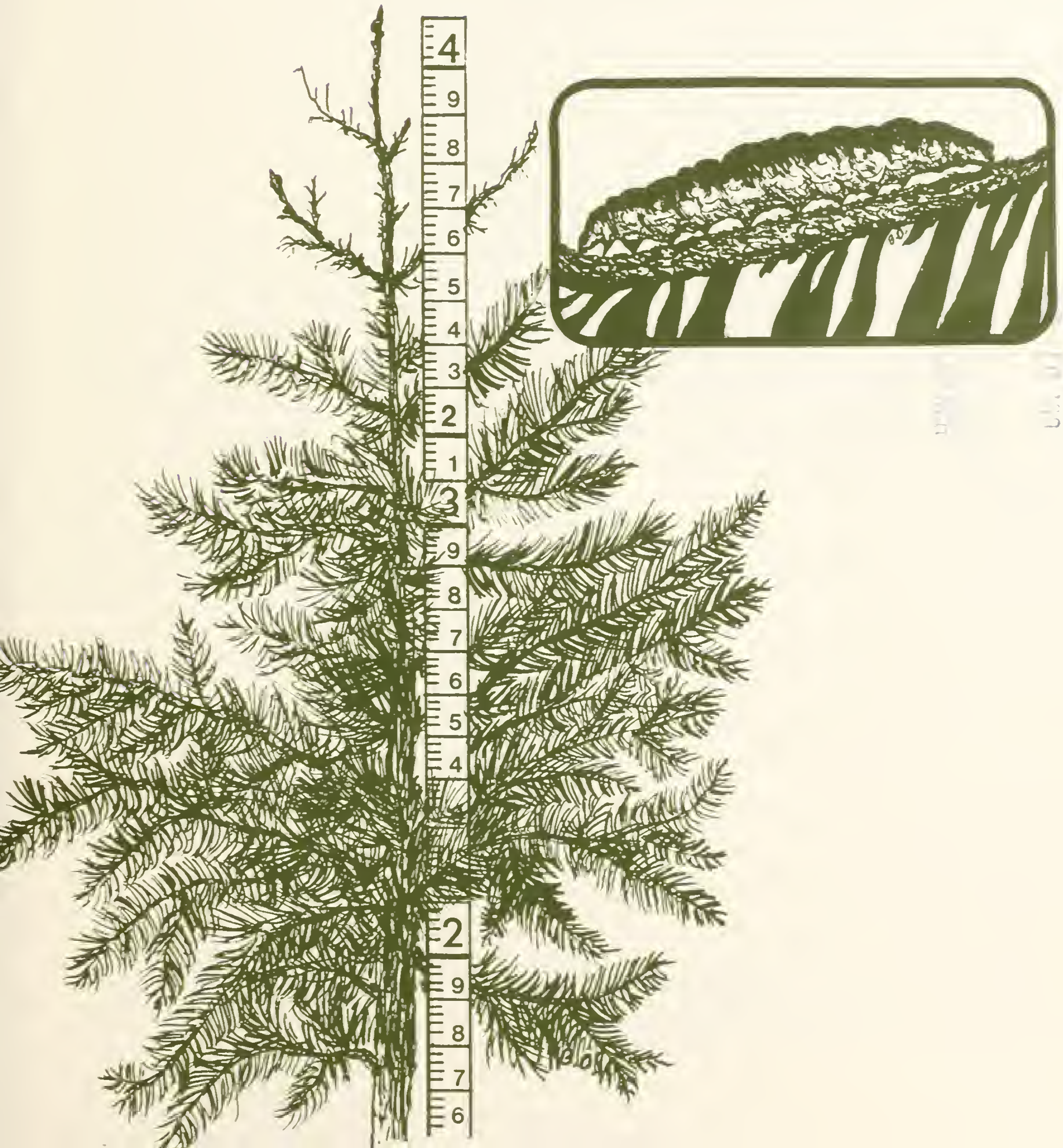

THE AUTHOR

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RESEARCH SUMMARY

Mathematical equations for predicting growth and development of four conifer species defoliated by western spruce budworm in Idaho are presented. Combinations of regeneration systems, ecological conditions, and defoliation levels were sampled to ensure that equations have broad applicability. A modeling strategy is provided to link these equations to growth and yield models so that short-term and long-term impacts can be assessed.

The research addresses budworm effects on four major features of regeneration development—dieback, height growth, crown ratio, and mortality. Backdating was used to characterize trees at the start of the study, then trees were measured annually for 5 consecutive years. Eleven percent of the host trees had dieback during the 5-year measurement period. The probability of dieback increases with increasing defoliation, increasing tree height, and decreasing crown ratio. The amount of dieback varied from 0.0 to 6.4 feet (0 to 67 percent of tree height). Over the 5-year period, 86 percent of the host trees had positive height growth. Height growth is related to tree and site conditions as well as defoliation level. Both defoliation prior to and during the 5-year period were significant, with increasing defoliation being associated with less height growth. Budworm defoliation prior to the 5-year measurement period decreased crown ratio, but defoliation during the period was not significant. Only 3 percent of the trees died; thus the dataset was not large enough to develop a reliable mortality model. Indications are that small crown ratios or high defoliation levels increase the probability of mortality.

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INTRODUCTION

Defoliation by the western spruce budworm (*Choristoneura occidentalis* Freeman) affects growth and survival of host trees in western portions of the United States and Canada. Budworm reduces growth, crown volume, and cone crops, and increases top-kill, mortality, deformities, and predisposition to insects and diseases. Impacts of budworm defoliation on large trees have been studied in some detail (see reviews by McKnight 1965 and Johnson and Denton 1975, as well as reports by Ferrell and Scharpf 1982, Van Sickle and others 1983, Swetnam 1983, Beveridge and Cahill 1984, Alfaro and others 1985, and Sanders and others 1985).

Regeneration is also fed upon by western spruce budworm, but fewer studies have reported budworm effects on regeneration. Small trees have a greater proportion of current-year foliage than large trees, can have small crown ratios if growing as understory trees, and may receive a disproportionate amount of budworm dispersing from overstory trees (Johnson and Denton 1975). Understory regeneration is often defoliated sooner than larger trees. Conversely, regeneration growing in young, even-age stands, without nearby overstory trees, is minimally fed upon by budworm (Carlson and others 1985).

The study reported here was designed to quantify impacts of western spruce budworm feeding on host regeneration up to 3.0 inches diameter at breast height (d.b.h.). The primary objective was to develop mathematical equations predicting 5-year periodic height growth of host regeneration as a function of species, tree condition, site/stand characteristics, and budworm defoliation. Additional information was gathered on dieback, mortality, and changes in crown ratio. Results apply to four species of host regeneration in budworm outbreak areas in Idaho. Host species are Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco), grand fir (*Abies grandis* [Dougl. ex D. Don] Lindl.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.). Questions regarding the probability of regeneration being defoliated by budworm are not addressed by this study.

STUDY DESIGN

Height growth of small trees can be backdated by measuring the height increment indicated by branch whorls. Often, this is not possible when growth is altered by budworm feeding. Top dieback and destroyed terminals being replaced by lateral branches can make it impossible to retrospectively determine height increments. Defoliation is difficult to backdate beyond a few years because branching pattern is abnormal and entire cohorts of needles may be missing. Therefore, this study was designed to follow growth and defoliation concurrently, although some backdating would be necessary to characterize the tree at the beginning of the study period.

Data were collected so that predictive equations would apply to a wide range of ecological conditions, defoliation levels, and current cultural practices. Active budworm outbreak areas were visited to establish semipermanent plots having combinations of ecology, defoliation, and silviculture of interest. Stands were selected by qualified research silviculturists using the following guidelines:

1. The stand was a relatively homogeneous area of at least 1 acre on which host regeneration up to 3.0 inches d.b.h. was established.
2. The last disturbance to the stand was at least 5 years ago. This 5-year period allows trees to adjust to changes in conditions caused by prior disturbances.
3. The stand was in a current budworm outbreak area. Defoliation levels by stand and by trees within stands were often quite variable.
4. With one geographic area (a Ranger District), stands were chosen to differ in such things as habitat type, host species, tree sizes, aspect, overstory density, or infestation level. This helped ensure dispersal of sampled conditions.

Extensive measurements were recorded in stands as of the beginning and end of a 5-year period. In addition, the stands were visited each fall to record current-year defoliation, height growth, and mortality. Variables recorded and timing of measurements are summarized in table 1. Plot installation began in the summer of 1979. Conditions as of the spring of 1978 were backdated by recording defoliation as of 1 year ago, height as of 1 year ago, and so on. Thus 5 years of information was gathered during four field seasons.

Ten-point clusters were used to sample stands. Each point is the center of a 1/300-acre circular fixed area plot and the center for a horizontal point sample. In stands with an overstory, basal area factors of 10, 20, or 40 ft^2/acre/tree were used to sample about five to seven overstory trees per point. Basal area factors were not changed between points within a stand.

The 1/300-acre plot was used to sample trees less than 3.0 inches d.b.h. and assess competition from shrubs, forbs, and grasses. All established conifers on this plot were recorded. Minimum establishment heights were

Table 1—Variables and frequency of measurement for three tree size classes. The 1978 measurements were recorded as the plots were installed prior to August 1979

Variable	Tree size class (d.b.h.) 0-2.9 inches	3.0-4.9 inches	≥5.0 inches	Year(s) recorded 1978	1979	1980	1981	1982
Identification field	x	x	x	√	√	√	√	√
Best tree	x			√				
Advance/subsequent	x			√				
Crown class relative to:								
A trees	x	x	x	√				√
B shrubs	x			√				√
Excess tree count	x			√				√
Yearly height increment	x			√	√	√	√	√
Current height	x	x	x	√				√
Height to dead or broken top	x	x	x	√	√	√	√	√
Crown dimensions	x	x		√				√
Vigor rating	x	x	x	√				√
D.b.h.	x	x	x		√			√
Dead/alive	x	x	x		√	√	√	√
Defoliation by crown thirds	x	x	x	√	√	√	√	√
Other:								
shrubs, forbs, grasses				√				√
damage/diseases	x	x	x	√	√	√	√	√
increment cores		x	x					√

0.5 ft tall for shade-tolerant species and 1.0 ft tall for shade-intolerant species. A subsample of "best trees" was selected on each plot, using the following set of rules:

1. Select the two trees most likely to survive and grow well, regardless of species.
2. Of each additional species, select one tree that is most likely to survive and grow well.
3. If rules 1 and 2 do not result in at least four trees, reselect from the remaining trees until four are selected, or until all trees have been considered.

Best trees were the sampling unit for this study. These trees were the most likely to produce a product later in the rotation. Sampling at least one tree of each species allowed for different growth rates among species as trees differentiate into crown classes. Sampling one tree of each species also meant that the best available host trees were included in the sample.

Best trees were tagged and measured for height (nearest 0.1 ft), height to dead or broken top (0.1 ft), crown dimensions (0.1 ft), d.b.h. (0.1 inch), crown class relative to (a) trees and (b) shrubs, advance or subsequent germination status relative to last stand disturbance, mortality, damages/diseases, height increments (0.01 ft), and ocular estimates of current-year defoliation.

Current-year defoliation was recorded each fall for best trees and tagged trees in the horizontal point sample. Crowns were divided into thirds—upper, middle, and lower—with the terminal rated separately for best trees. Binoculars were used to aid estimates in crowns of overstory trees. Defoliation was determined by ocularly estimating the proportion of current-year needles destroyed by budworm feeding. Estimates were rounded to the nearest 10 percent. Defoliation on each third of the crown was evaluated retrospectively for 1976, 1977, and 1978. Defoliation and height growth were estimated each fall in the years 1979, 1980, 1981, and 1982.

Regeneration not chosen as best trees was called "excess" trees and was counted by species and 1-ft height classes. Shrubs, forbs, and grasses were characterized by recording average height and percentage of plot coverage for species covering at least 5 percent of the plot.

Trees in the horizontal point sample were tagged and measured for height, crown class, height to dead or broken top, crown ratio, mortality, and defoliation by crown thirds. These trees characterize the effect of overstory competition on growth of regeneration. Diameter at breast height was recorded in the fall of 1979 and 1982, and increment cores were extracted in the fall of 1982. Results of analysis of large trees will be published separately.

Stand variables include geographic location, aspect, slope percent, elevation, topographic position, and habitat type. Habitat type references used were Cooper and others (1987) for northern Idaho, Steele and others (1981) for central Idaho, and Steele and others (1983) for eastern Idaho.

Ten-point clusters were installed in 64 stands (fig. 1). Stands in northern Idaho were clustered in areas near Avery and Powell. The outbreak in central Idaho covered a wider geographic area, allowing better distribution of sample stands. In 1979 few Douglas-fir climax stands could be found having the necessary combinations of silviculture, host trees, and defoliation. For this reason, five moderately to heavily defoliated stands were sampled in eastern Idaho. Table 2 shows the number of stands by regeneration system and overstory climax series (the most

Figure 1—Study site location for 64 sample stands.

Table 2—Number of stands sampled by overstory climax series and regeneration method. Each stand contains data from a cluster of ten 1/300-acre plots, with corresponding horizontal point sample of the overstory

Overstory climax series	Regeneration method	Number of stands
Douglas-fir	clearcut/seedtree	4
	shelterwood/selection	3
Grand fir and redcedar (*Thuja plicata* Donn. ex D. Don)	clearcut/seedtree	14
	shelterwood/selection	9
Subalpine fir	clearcut/seedtree	18
	shelterwood/selection	16
Total		64

Table 3—Attributes of 64 stands sampled for impacts by western spruce budworm on host regeneration

Attribute	Unit of measure	Mean	Standard deviation	Extreme values
Elevation	Nearest 100 feet	52.4	8.3	37.0 to 76.0
Aspect	Degrees	187	114	0 to 360
Slope	Percent	35.6	19.1	0.0 to 70.0
Overstory density	Ft²/acre at breast height	44.0	43.3	0.0 to 236.0

shade-tolerant conifer able to maintain a self-reproducing population; Daubenmire 1966). Table 3 shows additional attributes of the 64 sample stands.

Douglas-fir, grand fir, Engelmann spruce, and subalpine fir are the primary species fed upon in these stands. Western larch (*Larix occidentalis* Nutt.) is also a host species, but few trees were found in the sample stands. On larch, budworm severs terminal leaders and lateral branches; thus one budworm can have a large impact. On species other than larch, budworms mainly feed on new needles and buds, and the impact of individual worms is much less (Fellin and Schmidt 1967; Schmidt and Fellin 1973).

MODELING TECHNIQUE

This study quantified four major impacts to host regeneration:

1. Probability of dieback (zero or negative 5-year growth).
2. Amount of dieback.
3. Five-year periodic height increment.
4. Crown ratio changes.

The term "dieback" refers to top-kill from which trees can recover to produce a merchantable product above the point of top-kill. "Top-kill," as used in the Prognosis Model (Wykoff 1986), refers to a truncated height above which no merchantable volume will accrue.

Information collected on mortality is discussed, but more data are needed to develop a predictive model.

Equations quantifying these impacts will be used in the Budworm Prognosis Model (Crookston 1985). A diagram of one Budworm Prognosis Model cycle is presented in figure 2. Each cycle accounts for growth and dieback. Crown ratios also change, partly the result of budworm defoliation. The new crown ratio represents an index of vigor carried over to the next projection cycle.

Equations were developed using REX, a linear regression package (Grosenbaugh 1967) and RISK, a nonlinear regression algorithm (Hamilton 1974). RISK is an algorithm for dichotomously distributed dependent variables (for example, a tree did or did not have dieback). The form of the equation for RISK is

$$P = (1 + e^{-(\Sigma B_i X_i)})^{-1} \quad (1)$$

Probability (P) is continuous and bounded within the interval [0,1]. Goodness of fit for coefficients in linear and nonlinear equations was evaluated at the 0.05 significance level.

A 1-year delay was hypothesized between defoliation and its impact on regeneration height growth. This delay was based on knowledge that height growth of species with predetermined buds is correlated with conditions existent during bud formation (Kozlowski 1964) and that photosynthates for terminal bud expansion come mainly from 1-year-old foliage (Kozlowski and Winget 1964). Preliminary equations were tested using a 1-year delay versus no delay, and no differences were apparent. Because budworms feed on current-year terminal buds and terminal leaders, a delayed effect of defoliation may be masked. Independent variables representing defoliation are averages with no delay assumed between defoliation and impact on growth. Two averages were calculated—one for the 5-year measurement period of this study (1978 through 1982), and one for the 2-year period prior to the study period (1976 and 1977).

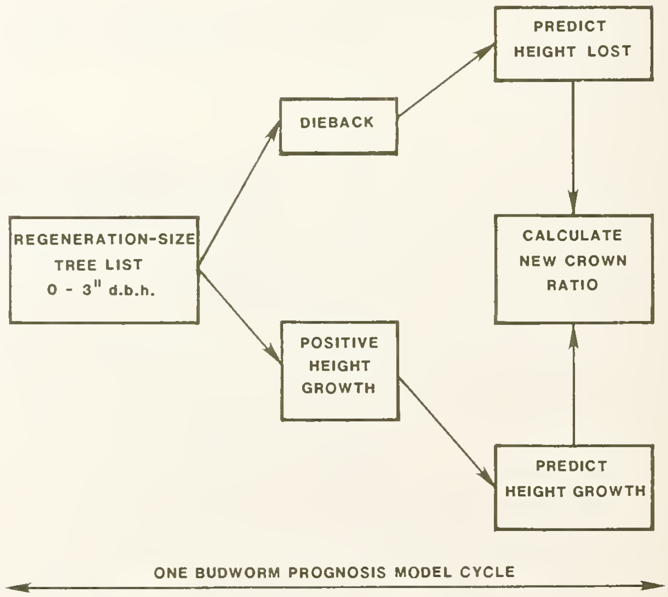


Figure 2—Diagram of steps to process regeneration for one cycle in the Budworm Prognosis Model.

Table 4—Attributes of sample trees by species and status at end of sampling period

Species	Number of trees	Beginning height (ft) Mean	Min-max values			Height increment (ft) Mean	Min-max values			5-year defoliation (percent) Mean	Min-max values			Beginning crown ratio Mean	Min-Max values		
								Status: Positive 5-year height increment									
Douglas-fir	215	5.0	0.1	to	23.2	1.5	0.1	to	7.7	19.9	0.0	to	85.3	0.58	0.03	to	1.00
Grand fir	444	4.2	.5	to	16.5	1.3	.1	to	8.8	19.3	.0	to	99.3	.55	.05	to	.96
Engelmann spruce	157	4.1	.6	to	14.0	1.7	.1	to	7.1	12.8	.0	to	82.0	.66	.15	to	.98
Subalpine fir	205	4.9	.5	to	16.8	1.8	.1	to	7.8	15.4	.0	to	84.0	.64	.12	to	1.00
Total	1,021																
								Status: Zero or negative 5-year height increment									
Douglas-fir	37	7.0	1.0	to	18.0	–.4	–3.0	to	.0	30.6	.0	to	92.0	.47	.08	to	0.94
Grand fir	55	6.6	.7	to	30.0	–.5	–5.0	to	.0	44.1	.0	to	92.7	.45	.18	to	.78
Engelmann spruce	9	5.6	1.5	to	11.9	–.3	–1.0	to	.0	27.0	2.0	to	79.3	.49	.24	to	.82
Subalpine fir	26	5.6	1.1	to	11.4	–.6	–6.4	to	.0	56.6	11.3	to	95.3	.55	.14	to	.96
Total	127																
								Status: Dead at end of 5-year measurement period									
Douglas-fir	12	6.3	1.3	to	11.0					18.8	.0	to	85.3	.48	.11	to	0.76
Grand fir	11	2.8	.5	to	7.3					25.0	.7	to	96.7	.42	.14	to	.68
Engelmann spruce	5	9.8	4.2	to	18.0					22.5	.7	to	83.7	.36	.28	to	.48
Subalpine fir	7	6.7	2.5	to	15.5					42.5	.0	to	93.3	.46	.29	to	.62
Total	35																
Grand total	1,183																

Defoliation estimates were backdated for the years 1976, 1977, and 1978. These estimates were recorded during the summer of 1979 as plots were being installed. It is possible that estimates of backdated defoliation could differ from the estimates made at the end of each growing season in 1979 through 1982. Variation, by species, between the backdated estimates and the current-year estimates was compared. The standard deviation of mean annual defoliation ratio for backdated estimates varied from 0.20 to 0.33 and averaged 0.27 for 12 observations (four host species times 3 years). The standard deviation for current-year estimates varied from 0.19 to 0.35, averaging 0.27 for 16 observations (four host species times 4 years). Thus, the backdated estimates are consistent with the prospective estimates. Backdating defoliation 3 years seems acceptable, considering that the 3-year period is less than the number of years of needle retention for these species, and field crews could get close to regeneration-size trees to accurately examine the cohorts of needles.

RESULTS AND DISCUSSION

A total of 1,183 host trees were measured for the entire 5-year period of this study. Of these, 127 trees (11 percent) suffered dieback and 35 (3 percent) died. Table 4 summarizes statistics for best trees by status at the end of the 5-year measurement period. These data are characterized by a wide range of values for the attributes shown. Compared to trees having positive growth, trees with dieback tended to be taller, had more defoliation over the 5-year period, and had smaller beginning crown ratios. This trend is also true of the 35 trees that died.

Trees were categorized by their status at the end of the 5-year measurement period—those having positive height increment, those having dieback, and those that died. Regression equations were then developed by status. Definitions for dependent and independent variables used in the regression equations are given in table 5.

Probability of Dieback

Dieback is defined as trees having zero or negative height increment for the 5-year period of this study. The event of dieback is distributed dichotomously; that is, a tree had dieback or it did not. All trees alive at the end of 5 years were used for this analysis, and RISK was used to estimate coefficients for the probability of dieback. Table 6 lists the coefficients and figure 3 shows comparative curves for various tree and defoliation conditions.

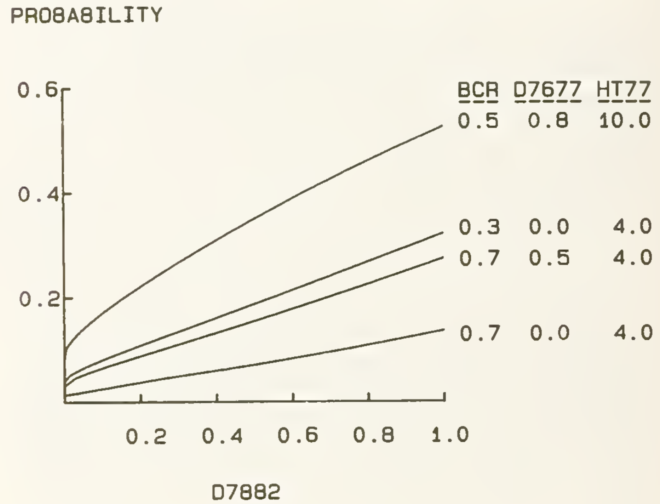
Important predictors of dieback are defoliation prior to and during the measurement period, beginning crown ratio, and beginning height. Defoliation during the 5-year period increased the probability of dieback more than defoliation prior to the period, although both are significant at the 5 percent level. Taller trees and those with smaller crown ratios have greater odds of sustaining dieback. There were not significant differences among the four species. Also crown class was not important when included in addition to the independent variables shown in table 6.

Table 5—Explanation of variables used in developing equations

Variable	Definition
BCR	Beginning crown ratio, measured during the summer of 1979.
D7677	Average defoliation ratio of current-year foliage for 1976 and 1977 (defoliation prior to measurement period).
D7882	Average defoliation ratio of current-year foliage for 1978 through 1982 (defoliation during the measurement period).
HT77	Tree height (ft) in the fall of 1977 (beginning tree height).
HT82	Tree height (ft) in the fall of 1982 (ending tree height).
BA	Overstory basal area in the fall of 1982 (ft^2/acre at breast height).
ASP	Aspect in radians.
SLO	Slope tangent (slope percent divided by 100).
ELEV	Elevation above sea level to the nearest hundred feet, for example, 35 = 3,500 feet.
TPP	Number of trees less than 3.0 inches d.b.h. on the fixed plot.
DBH82	Tree d.b.h. in the fall of 1982.
ADVANCE	Class variable for advance regeneration ADVANCE = 1.0 if the tree is older than the last stand disturbance; 0.0 if the tree is not advance.
DIEBACK	Class variable for trees having zero or negative net height increment over the 5-year measurement period.
HTI	Positive 5-year periodic height increment (ft).
CR	Ending crown ratio, measured in the fall of 1982.
CROWN CLASSES	
DOMINANT	Crown receiving sunlight from above and three or four sides.
CODOMINANT	Crown receiving sunlight from above and one or two sides.
INTERMEDIATE	Crown receiving sunlight only from above.
SUPPRESSED	Crown not receiving sunlight from above or sides.
SPECIES	
ABGR	*Abies grandis*
ABLA	*Abies lasiocarpa*
ACGL	*Acer glabrum*
CLUN	*Clintonia uniflora*
MEFE	*Menziesia ferruginea*
PSME	*Pseudotsuga menziesii*
SPBE	*Spiraea betulifolia*
THPL	*Thuja plicata*
VAGL	*Vaccinium globulare*
VASC	*Vaccinium scoparium*
XETE	*Xerophyllum tenax*

Table 6—Coefficients for equation predicting the probability of dieback (P) for budworm defoliated regeneration. Form of the equation is $P = [1 + e^{-(\Sigma \beta X)}]^{-1}$. The t-ratios for all coefficients were significant at the 5 percent level

Variable (X)	Coefficient (β)
β_0	–2.5817
BCR	–2.7635
$\sqrt{D7677}$	1.2394
$\sqrt{D7882}$	2.4696
HT77	.0488



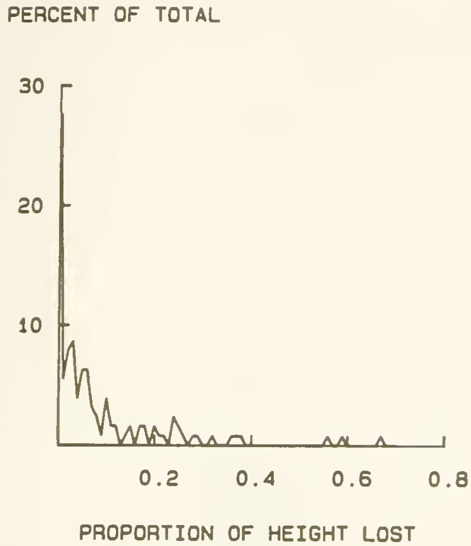


Figure 4—Distribution of the proportion of height lost for trees having dieback. Proportion = length of dieback ÷ beginning tree height.

Amount of Dieback

Using the 127 trees that had dieback, combinations of dependent and independent variables were explored to predict the amount of height loss. Dependent variables included length of top-kill, proportion of height lost, and proportion of crown ratio lost. The only significant independent variables in these linear regression equations were tree height, crown length, and slope, but their predictive value was very low.

Part of the problem in predicting the amount of dieback is that the loss is only a "snapshot" at one particular time during an ongoing infestation. Dieback could increase or decrease, depending on current and future defoliation levels.

Another explanation is found in the frequency distribution of the proportion of height loss shown in figure 4. Most of the trees had no net loss over the 5-year period. These trees are followed in frequency by fewer and fewer trees with increasing losses. Regression equations tend to predict near the mean loss, resulting in large errors of prediction.

Because the amount of dieback is highly variable, effort was directed toward quantifying the distribution associated with the loss. A Weibull function (Bailey and Dell 1973) was fit to the data points of figure 4. The cumulative distribution function (*CDF*) is

$$CDF = 1 - e^{-[(PD/5.684)^{0.587}]} \tag{2}$$

where *PD* is proportion of total tree height lost to dieback.

In a growth and yield simulation where growth projections are made for individual trees, the equation shown in table 6 is used to determine which trees lose tops. For each tree having dieback, a uniformly distributed random number is chosen in the interval [0,1] and substituted for *CDF* in equation (2). The equation is then solved for *PD*, the proportion of dieback. The simulated distribution approximates the actual distribution, given that enough trees are in the inventory. The Prognosis Model (Stage 1973) ensures an adequate number of trees by replicating tree records.

Height Growth

Overall, 1,021 (86 percent) of the sample trees had positive height increments as determined by subtracting height in 1977 from height in 1982. Although yearly increments had been recorded, it was not accurate to sum these over the 5 years because lateral branches often turned up to replace shorter, defoliated terminal shoots. When lateral branches replace terminals, tree height can increase even when defoliation is quite heavy.

The four species were analyzed separately. Important independent variables were identified through screening analysis using REX. Likely transformations of independent and dependent variables were explored. The shape of the response surface for defoliation was examined by dividing defoliation into discrete groups (0 to 5 percent, 5 to 15.5 percent, 15.5 to 26.5 percent, ..., 56.6 to 65.5 percent, and ≥65.5 percent) to be used as class variables. A coefficient was estimated for each class while using the most important tree, site, and stand conditions as covariates. The results were plotted and are shown in figure 5. The response surface for regression coefficients is linear and negative when plotted on the log scale.

Final equations were developed after including species-specific effects such as habitat type, geographic location, or elevation (table 7). The form of the equation is

$$\ln(HTI) = B_0 + B_1X_1 + B_2X_2 + ... + B_iX_i \tag{3}$$

where

HTI = 5-year height increment
B_i = regression coefficients
X_i = independent variables.

This equation form was the best transformation found when screening the data and has been used in predicting regeneration height growth by Wykoff and others (1982). The effect of defoliation is shown graphically in figure 6.

Taller trees and those with larger crown ratios grow better than shorter trees or those with smaller crown ratios. Both defoliation prior to and during the growth period significantly reduce height growth of regeneration-size trees, but the current defoliation has a greater effect. Increasing overstory basal area reduced expected height increment, and the reduction is greater for the moderately shade-tolerant Douglas-fir and Engelmann spruce than it is for shade-tolerant grand fir and subalpine fir.

Crown Ratio

Crown ratio is an indicator of tree vigor because it indexes the amount of foliage available to produce photosynthates. Spruce budworm defoliation reduces the foliage density and crown ratio which, in turn, impact future

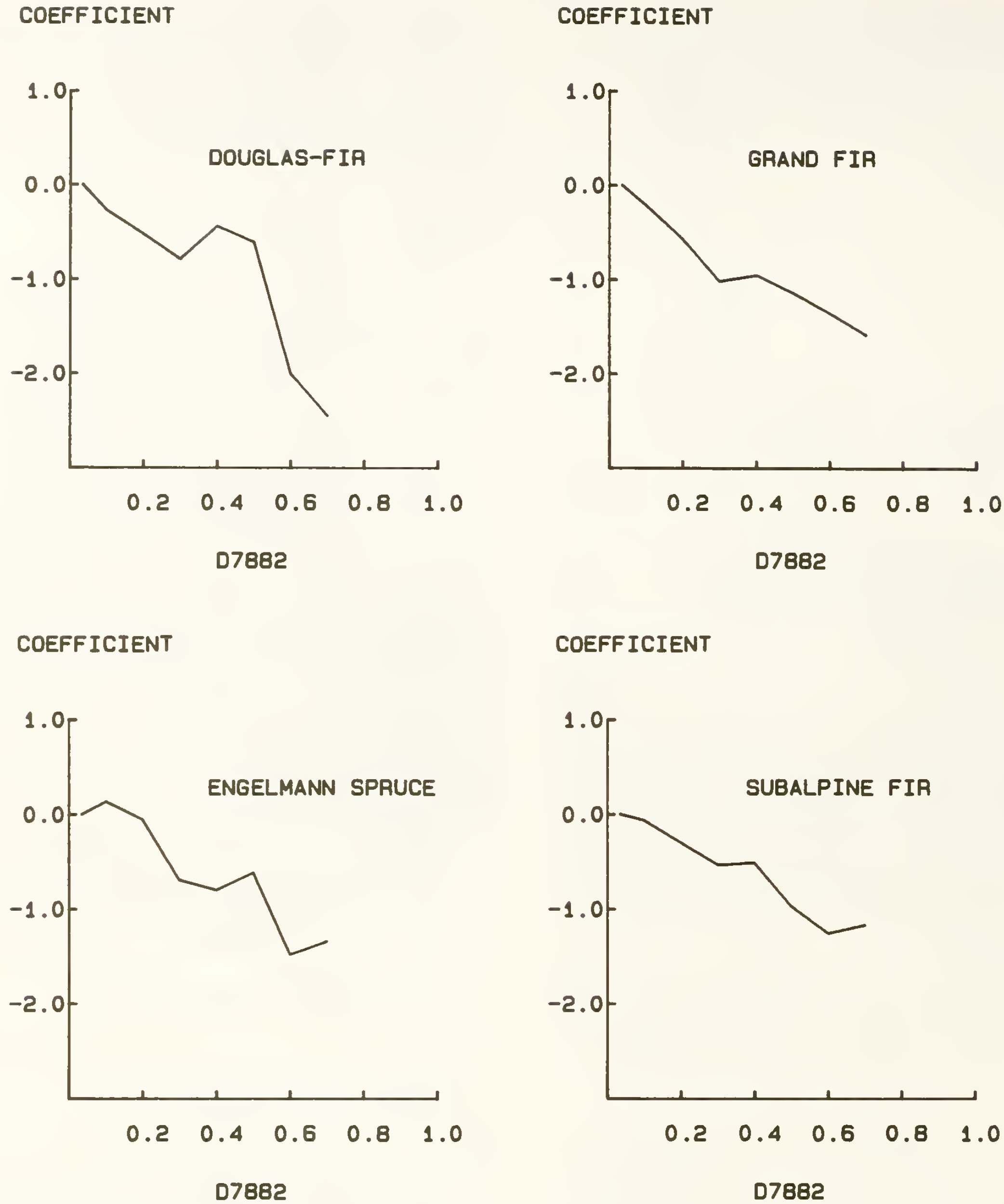


Figure 5—Regression coefficients predicting height growth by defoliation class and species. Results are linear when plotted on the natural logarithmic scale.

Table 7—Coefficients for equations predicting height increment (HTI) for 1,021 trees having positive height increments over the 5-year period. The form of the equation is $\ln(HTI) = \Sigma\beta_i X_i$. Equations are for trees up to 3.0 inches d.b.h.

Variable (X)	Douglas-fir (β)	Grand fir (β)	Engelmann spruce (β)	Subalpine fir (β)
β_0	0.1137	1.1714	–2.3558	–1.1306
ln(HT77)	.5991	.5173	.5610	.7452
BCR	1.6987	1.7175	1.7423	.8682
ln(BA)	–.1150	–.0428	–.1415	–.0709
D7882	–1.5133	–1.3745	–1.8405	–1.4359
D7677	–.9624	–.6263	–1.0766	–.9302
COS(ASP)*SLO	.4544	–.0152		
SIN(ASP)*SLO	.3995	.2820		
SLO	–.0506	.7228		.7320
ELEV	–.0207	–.0165	.0241	
ADVANCE		–.1948		
FORESTS				
PAYETTE		.5981	.2410	
BOISE		.8354	.9165	
PANHANDLE		.0	.2410	
CLEARWATER		.0	.0	
TARGHEE		[1]	[1]	[1]
HABITAT TYPES				
PSME series		[1]	[1]	[1]
ABGR/SPBE		–.5965	[1]	
ABGR/VAGL		–.5965	–.5558	[1]
ABGR/CLUN		.0	.0	
ABGR/ACGL		–.5965	[1]	[1]
THPL/CLUN		.0	.0	
ABLA/CLUN		.0	.0	
ABLA/MEFE		–.5965	–.5558	
ABLA/XETE		–.5965	–.5558	
ABLA/VAGL		–.5965	–.5558	
ABLA/VASC		–.5965	–.5558	
CROWN CLASS				
DOMINANT		.6485	.2714	
CODOMINANT		.5588	.1084	
INTERMEDIATE		.4750	.0	
SUPPRESSED		.0	.0	
No. of trees	215	444	157	205
r^2	0.5204	0.5979	.6631	0.6451
Standard error of estimate	.8193	.6495	.5708	.6671

[1]No data for this cell.

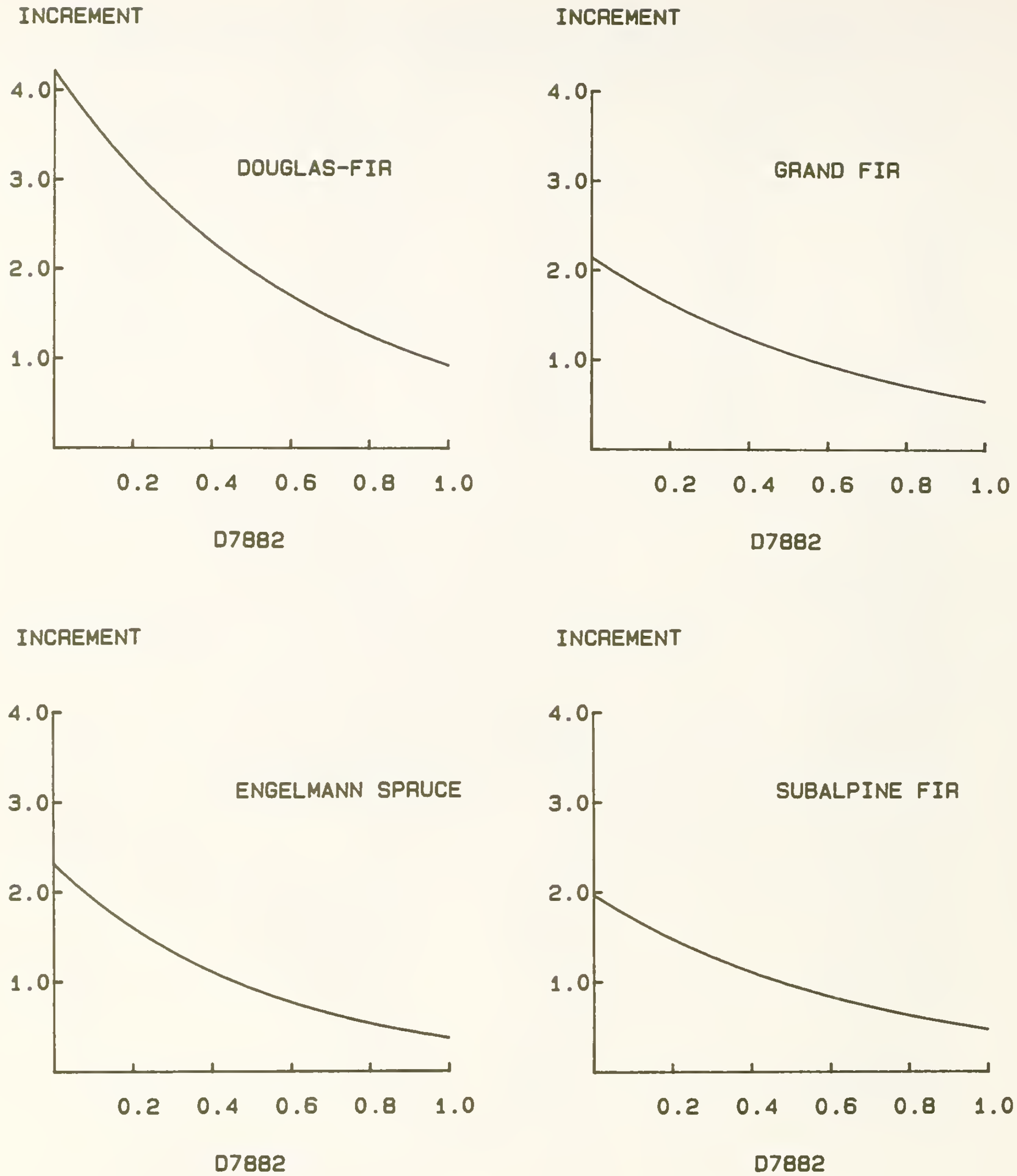


Figure 6—Predicted 5-year height increment (feet) as a function of 5-year defoliation and species. Graphs were developed using the equations shown in table 7. Variables held constant in the equations are HT77 = 5.0, BCR = 0.7, BA = 1.0, D7677 = 0.0, ASP = 0.0, SLO = 0.0, ELEV = 40.0, ADVANCE = 0.0, Clearwater National Forest, THPL/CLUN habitat type, and codominant crown class.

Table 8—Coefficients for equations predicting crown ratio (CR) at the end of the 5-year measurement period. Equations are for trees with positive height growth and those suffering dieback. The form of the equation is shown in equation 4

Variable X	Douglas-fir (β)	Grand fir (β)	Engelmann spruce (β)	Subalpine fir (β)
β_0	−1.2675	−0.7396	−1.1142	−0.9827
ln(HT82)	.1615	.3353	.4405	
ln(BA)	−.1085	−.0408	−.1084	
COS(ASP)*SLO	−.4233			.6411
SIN(ASP)*SLO	.1974			−.3264
SLO	.4292			.3482
D7677	−.5402	−.6442	−.8326	−.6892
ln(TPP)		−.1059		
BCR	2.4368	2.4586	2.8443	2.8178
ADVANCE		−.2473	−.2693	
CROWN CLASS				
DOMINANT	.8636	.4688		.6417
CODOMINANT	.6543	.4304		.2698
INTERMEDIATE	.4419	.3436		.3377
SUPPRESSED	.0	.0		.0
DIEBACK		−.3766		−.3551
No. of trees	252	499	166	231
r^2	.6104	.5780	.5874	.6006
Standard error of estimate	.6152	.6327	.6289	.6935

growth, dieback, and mortality. When estimating crown ratios, field crews made ocular adjustments for trees having one-sided crowns or missing portions of crowns, but no adjustments were made for the sparseness of crowns caused by defoliation. Thus crown ratio is that proportion of tree height that would refoliate if budworm feeding stopped.

Equations were developed to predict crown ratio at the end of the measurement period. The form of the equation is

$$CR = [1 + e^{-(\Sigma B_i X_i)}]^{-1} \qquad (4)$$

where

CR = crown ratio
B_i = regression coefficients
X_i = independent variables,

which is a sigmoid-shape curve bounded within the interval [0,1]. Coefficients are shown in table 8. The most important variables are crown ratio at the beginning of the period, defoliation prior to the beginning of the measurement period, overstory basal area, tree size, and crown class in relation to other trees. Trees with larger beginning crown ratios had larger ending crown ratios, but prior budworm defoliation decreased crown ratios. Increasing overstory basal area decreased crown ratios, and larger trees had larger crown ratios. Also, the more dominant the tree relative to other trees, the larger the crown ratio. Defoliation during the measurement period was not significant, indicating a delay between defoliation and reduction in crown ratio. Geographic area, habitat type, and crown class in relation to shrubs were not significant.

Mortality

Only 3 percent of the trees died during the 5-year measurement period of this study. The dataset is too small to develop a reliable equation predicting the probability of mortality, but single independent variable equations were fit to the data using RISK. Crown ratio at the beginning of the measurement period was a significant variable. Trees with small crown ratios have a higher probability of mortality. Defoliation prior to the measurement period was also significant, with increasing defoliation causing increasing mortality. Defoliation during the 5-year period was not significant. A delay between defoliation and mortality has been described by others (Beveridge and Cahill 1984; McLintock 1955).

SUMMARY

This study was undertaken to quantify the impacts of western spruce budworm defoliation on growth and development of young conifers. Equations presented in this paper can be embedded in the Budworm Prognosis Model (Crookston 1985) or other growth and yield simulation models. Through use of simulation models, alternative management prescriptions can be compared.

This study has quantified four major effects of budworm defoliation on regeneration: (1) probability of dieback, (2) amount of dieback, (3) 5-year periodic height increment, and (4) changes in crown ratio.

The probability of dieback increases with increasing defoliation, smaller beginning crown ratios, and increasing tree size. Still, only 11 percent of host regeneration had dieback. Even with heavy defoliation, lateral branches or buds replace terminal shoots destroyed by budworm and, as shown in figure 4, the proportion of height lost is usually low.

Periodic height increment is also reduced by budworm feeding. Defoliation prior to and during the growth period significantly reduces predicted 5-year height increment. Crown ratio is important in that trees with small crowns grow less and, as shown in the crown ratio equations, budworm feeding has a delayed effect on reducing the crown ratio of defoliated trees.

Defoliation prior to the 5-year measurement period is a good predictor of crown ratio at the end of the period. Increasing defoliation prior to the growth period results in smaller crowns, but defoliation during the growth period is not significant.

Few host trees died during the 5-year period of this study. Mortality increases as crown ratio decreases or prior defoliation increases, but the dataset was not large enough to develop a reliable equation.

Several equations in this paper use crown class to help predict growth and development of regeneration. These discrete classes would be appropriate for short-term projections in growth and yield simulations where the list of trees is from a stand inventory. But information is lacking on movement of trees from one class to another as the stand develops and trees differentiate over time. Discrete classes can also produce irregular growth rates as trees pass from one crown class to another. A surrogate is needed to represent the effect of crown class for regeneration-size trees.

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Mathematical equations are presented for predicting growth and development of regeneration as a function of species, tree condition, site characteristics, and western spruce budworm defoliation. The dataset consists of 1,183 host trees on which growth and defoliation were followed concurrently for 5 years. Probability of dieback is positively related to defoliation and negatively related to crown ratio. Height growth is negatively related to budworm defoliation and positively related to crown ratio. Crown ratio decreases with increasing defoliation, but the effect is delayed. Indications are that the probability of mortality is positively related to defoliation and negatively related to crown ratio.

KEYWORDS: *Choristoneura occidentalis*, reproduction, modeling, succession, forest management, planning

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